Physiological adaptations in the Rosy Pastor wintering in India[1]

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INTRODUCTION

The physiology of bird migration has been the subject of extensive investigation for many years in my former laboratory at the Maharaja Sayajirao University of Baroda (latitudes 20-24 and longitudes 72-76), Gujarat, India. The Rosy Pastor or the Rosecoloured Starling [*Sturnus roseus* (Linnaeus)] has been one of the most intensively studied species of migrants wintering in the area. With the establishment of a centre for the study of the physiological basis for animal migrations at the University of Guelph in Canada, it has become possible to collaborate with former colleagues at Baroda in continuing some of the studies and also extending them to species of the northern hemisphere.

In any physiological investigation on a wild species, reliable field information regarding its distribution and natural history is a prerequisite. In my own studies on the Rosy Pastor as well as on other species of Indian birds, I have had to draw constantly from Sálim Ali's experience. On occasions when he pulled me out into the field with him, he generously shared with me his incredible enthusiasm and wealth of knowledge. I consider this opportunity of associating myself in the felicitations on the occasion of his 75th birthday a unique privilege, since another one of his kind may never be.

According to Sálim Ali (1955), the Rosy Pastor is one of the earliest winter visitors to India, abundant in the north-western parts. They arrive in July-August and leave about the middle of April and return to their breeding grounds in eastern Europe, western and central Asia, where they nest in May and June. Their breeding is known to overlap that of the migratory locust, thus ensuring sufficient supply of food for themselves and their young.

On arrival in Baroda, they are greeted by the monsoon rains and plentiful supplies of insects as food. Toward their departure in late April, the ambient temperature in Baroda may go up as high as 110°F or more, after an intervening period of the cool tropical winter. Toward

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migration their diet becomes mostly, if not entirely, vegetarian consisting of banyan and pipal figs and various types of berries. The fruits of *Pithecolobium dulce*, locally called *goraz amli*, seems to be a major food item during the fattening period prior to migration. The difference in the day-length between the winter and spring (summer) months is relatively insignificant compared to that in the Temperate Zone. Nevertheless, the changing environmental conditions do impose on the bird the necessity of adaptational changes in the body.

NATURE OF ADAPTATIONS

The adaptational changes in the body of a migratory bird may be regarded as the result of a dialogue between the environment and the biological organization within. These changes evidently occur at various levels of organization, thereby affecting the physiology and behaviour of the organism as a whole. The physiologist therefore seeks to investigate the influence of environmental factors such as light, temperature, humidity etc., structural and metabolic adaptations, the mechanism of internal regulation which possibly determines the actual timing of migration and the processes involved in the generation and utilization of energy for migratory flight. These aspects of the physiology of the migratory bird embrace practically all basic life processes and the revelation of these principles should lead ultimately to an understanding of the very nature of life itself.

This review deals mainly with the work done, under the auspices of the M. S. University of Baroda, on the Rosy Pastor from the time of its arrival in Baroda to its departure for its breeding grounds abroad. The exact time of their arrival in Baroda is not known but small groups are quite common about September. This phase will be referred to as the postmigratory phase. Towards March, they flock together into larger groups and by April end, form large migratory swarms [see photograph by Sálim Ali (1955) ; Plate 72 facing p. 127]. This phase will be referred to as the premigratory phase. The adaptational changes occurring in the various tissue and organ systems will be considered under these two phases.

INTERNAL REGULATION

The hypothalamus is well recognized as the seat in the brain that controls numerous autonomic and endocrine functions. It contains neurosecretory cells some of whose secretions are transported to the hypophysis through portal circulation while others are stored and released from the neurohypophysis. The hypothalamus has also been shown to be controlling the regulation of food intake. A normal mature animal maintains its body weight fairly constant, which is indicative of a regulatory mechanism operating to balance energy intake with output. It has been demonstrated in several laboratory mammals that two areas in the hypothalamus are responsible for the regulation of food intake. The studies of the Indian physiologist B. K. Anand and his associates (1955) have provided experimental evidence to show that the lateral hypothalamic area is involved in increased daily food intake and the medial area in decreased food intake. It is well known that migratory birds deposit considerable amounts of fat in the body prior to migration. Rosy Pastors have been found to weigh 50-60 g in October and 80-125 g in April (Naik 1963) the increase in body weight being, by and large, due to the deposition of fat. Kuenzel & Helms (1967) have produced obesity in the migratory Whitethroated Sparrow by experimentally creating lesions in the ventro-medial area of the hypothalamus. In the light of these observations, the hypothalamus may be considered as not only the link between the brain and the endocrine complex but also as the site where the initial triggers, that control the sequence of events in effecting migratory activity, reside. George & Naik (1965) have described the hypothalamo-hypophysial neurosecretory system of the Rosy Pastor. The hypothalamic neurosecretory centres consist of the supraoptic and paraventricular nuclei, and the anterior and posterior divisions of the infundibular nucleus as revealed by staining with paraldehyde fuchsin as well as Gomori's chrome alum haematoxylin phloxin for neurosecretory material. The granular neurosecretory material presenting a beaded appearance was traced from the cell body along the axon to the regions of distribution and storage depots. The intensity of staining in the cells was considered an index of their secretory activity and that in the storage areas, the extent of accumulation of the neurosecretory material. On studying the intensity of staining of the neurosecretory material in birds collected during the postmigratory and premigratory phases, they observed certain definite cyclic changes. During the postmigratory phase (October/November), the amount of the neurosecretory material in the supraoptic and paraventricular nuclei, the median eminence and the neurohypophysis was found to be relatively low compared to that in the premigratory phase. Towards February, there was slight increase but no perceptible change was noticed until the end of March. From the last week of March, there was distinct increase, especially in the supraoptic and paraventricular nuclei, the tractus tubero-hypophysis and the neurohypophysis. The neurosecretory cells were found to be conspicuously larger with the nuclei and nucleoli also increased in size and surrounded by a larger amount of cytoplasm. The axons of the cells also were easy to trace due to their high content of neurosecretory material. A few days prior to migration, however, the neurosecretory material was found to be considerably depleted in the neurohypophysis, presumably released into the general circulation. The reduction in the neurosecretory material was also noticed in the other parts possibly released and dispersed into the anterior pituitary through the portal circulation. This release of the neurosecretory material was considered a trigger in initiating the chain of events that follow in the migratory process. In a study of the localization and intensity of the activity of the enzymes, acid and alkaline phosphatases in the hypothalamo-hypophysial system, Naik & George (1966) observed considerable increase in the enzyme activity towards migration time. They correlated these changes with increased production and release of the neurosecretory material. John & George (1970) studied histo-chemically the localization and intensity of lipase activity in the hypothalamo-hypophysial system in the post- and premigratory periods. The enzyme activity was found to be increased in the premigratory phase in the hypothalamic neurosecretory nuclei, median eminence, pars nervosa and adenohypophysis. The increase in the enzyme activity has been correlated with increased lipid metabolism in these regions.

If the release of the neurosecretory material were to influence the regulatory mechanism in the body, evidently significant changes in the master gland in the body, the anterior pituitary, should be expected. Extensive studies on the mammalian pituitary have shown the relationship between the various cell types and the hormones secreted by the gland. In a cytological study of the pituitary gland of the Rosy Pastor using histo-chemical staining techniques, Naik & George (1965a) distinguished six types of chromophil cells consisting of three types of acidophils : Small orange G cells (prolactin [LTH] cells), Large orange G cells and Acid fuchsin cells (ACTH cells) ; and three types of basophils : Purple cells (TSH cells), Deep green cells (FSH cells), Light green cells (LH cells). Functionally these cells are believed to be responsible for the production of the hormones indicated in brackets against each cell type. The cell type for the growth hormone could not be identified. A general increase in the number and activity, as indicated by size and staining intensity, was noticed in all cell types towards migration.

A few days prior to migration, the purple cells showed signs of degranulation. This coincided with the release of the colloid in the thyroid gland (George & Naik 1964a). A study of the serum tyrosine level which is indicative of thyroidal activity, by Pilo & George (1970a), showed that the peak level of 104 microgrammes per millilitre was reached towards migration time (last week of April).

The increase in the number of the deep green cells was found to be associated with the development of the testes in male (Naik & George 1964a). With the release of the colloid from the thyroid, the development of the testicular elements ceased at the stage of primary and secondary spermatocytes, to be resumed after migration at the breeding grounds. Parallel changes in the females were considerably slower, which probably accounts for the fact that females leave later.

Prolactin has been implicated as a factor in fattening leading to migratory activity. The increase in the small orange G cells is in accordance with this contention.

The increase in the acid fuchsin cells prior to migration was reflected in the increased production of corticoids in the adrenal towards migration (Naik & George 1963). Increased production of ACTH is also of significance since this hormone is known to be a fat-mobilizing hormone. The transport of fat from the adipose tissue to the muscles as a hormone-mediated process is now well established. Histological and histochemical studies (Naik & George 1965b) on the adrenal have demonstrated striking seasonal changes in the adrenal cortex. Towards migration there was considerable increase in the amount of RNA and fat and also in mitochondrial density, thus presenting a sort of hypertrophic condition in the cortex. These changes might have been influenced by increased ACTH production. The above changes in the adrenal were also found to be accompanied by increased activity of alkaline phosphatase in the cortex and of acid phosphatase in the medulla (Naik & George 1964b).

The ascorbic acid (Vitamin C) content of the adrenal was found to drop towards migration (John & George 1967b). They suggested that this drop in ascorbic acid might be a factor in stimulating the production of corticosteroids and adrenalin. Cholesterol is known to be a precursor of steroid hormones. John & George (1967a) found a marked increase in total cholesterol in the adrenal from February to April, the increase in February being significantly more than that in April. They suggested that cholesterol was being rapidly converted to corticosteroids with the aid of ACTH which was also expected to be significantly increased (Naik & George 1965a). The role of ACTH in the conversion of cholesterol to corticosteroids has been discussed by Hayano *et al.* (1956). In the production of adrenalin, tyrosine is known not be a precursor while phenylalanine is believed to have a role in the synthesis of adrenalin. In a study of the seasonal changes in the concentration of these two amino-acids in the adrenal, John & George (1967c) found that the peak was reached in the month of February and the trough towards migration time. This drop in the amino-acid level has been correlated with the decrease in ascorbic acid and also with increased production of adrenalin towards migration time.

The adipokinetic as well as hyperglycaemic function of glucagon and the hypoglycaemic function of insulin, the two hormones produced by the alpha and beta cells respectively in the islets of Langerhans of the pancreas, are well known. George & Naik (1964b) observed an increase in the number of islet cells mainly through the conversion of the acinar cells during the premigratory phase. With the increased activity of the beta cells the high blood-sugar level in the month of February began to decline, reaching a low in April, obviously with increased production of insulin. Consequently, the high sugar intake was diverted towards fat synthesis.

PREMIGRATORY FAT DEPOSITION

That migratory birds deposit large amounts of fat prior to migration is common knowledge. Fat mainly in the form of triglycerides is stored in the adipose tissue present in the different regions of the body, the abdominal fat pad being the most prominent. Unlike in mammals, the adipose tissue in the avian body is not known to be an active site for fat synthesis. Most of the synthesis of fat is believed to take place in the liver in birds. George & Naik (1963) discovered certain haematopoietic nodules in the liver of the Rosy Pastor which were also found to be sites of fat synthesis. These nodules were found to be most active in the production of different types of blood cells—erythrocytes, granular leucocytes, lymphocytes and monocytes, during the premigratory phase. Fat was found to be synthesized by the lymphocytes, monocytes and free moving reticulo-endothelial cells, the main synthesis being in the reticulo-endothelial cells. Though fat is not actively synthesized in the avian adipose tissue, the tissue as such has been shown to be a metabolically active tissue, much more so in the Rosy Pastor than in the domestic fowl (George & Eapen 1958, 1959). Naik (1963) studied the water, fat, protein and glycogen content of the liver of the Rosy Pastor in the post- and pre-migratory phases. He observed that the body weight increased from 51-58 g in October to 80-125 g in April prior to migration. While the water and protein contents of the liver decreased towards migration time, fat and glycogen content increased. The increase in body weight was by and large due to the deposition of fat in the adipose tissue. Blood fat in transit was also high towards migration time. An enzyme, lipase, known to be responsible for hydrolysing fat into fatty acid and glycerol and esterifying fatty acids and glycerol to glycerides, is also known to be a clearing agent for fat in the blood. George & Vallyathan (1961) studied the serum level of lipase activity in the domestic fowl, pigeon and the Rosy Pastor. They found that the Rosy Pastor had a serum lipase level about 10 times that of the domestic fowl and about twice that of the pigeon. The pigeon which is a good flier has a very much higher serum lipase level than a poor flier like the domestic fowl; while the Rosy Pastor, which is a migratory bird, has a considerably higher level than the pigeon.

Seasonal variation in the deposition of fat in birds in general, and the deposition of migratory fat in migratory birds in particular, is well documented (see George & Berger 1966). The role of fat as fuel for muscular energy during migration has been discussed at length by George & Berger (1966). The machinery necessary for metabolizing fat in the muscles therefore becomes a topic for consideration.

Fuel of muscle

It is well established that the fat content of the chief avian flight muscles, pectoralis and supracoracoideus, is generally higher than the muscles of most other animals (George & Berger 1966). In the Rosy Pastor the fat content of *M. pectoralis* is considerably increased towards migration (Vallyathan 1963). It should be mentioned here that the glycogen content of the muscle is also increased at the same time (Vallyathan & George 1964; George & Chandra-Bose 1967). It is possible that during the initial part of flight and also in short flights, carbohydrate would be the preferred fuel, thus sparing fat, and as flight is prolonged, fat would take over as the chief fuel. Even then, some carbohydrate would be metabolized, because the utilization of fat through fatty acid oxidation takes place in the ' flame ' of carbohydrate. Studies on pigeons subjected to electrical stimulation of the pectoralis muscle have shown that fat is transported from the adipose tissue to the muscle through the blood stream (George & Berger 1966; Vallyathan & George 1969; Vallyathan *et al.* 1970). If fat is to be utilized, it has first to be broken down to fatty acids and glycerol. The fatty acids are then oxidized in the mitochondria, generating free chemical energy in the form of adenosine tri-phosphate (ATP) as the main product and carbon dioxide and water as by-products. It is known that the flight muscles of birds contain a high concentration of the enzyme, lipase, which splits fat into fatty acids and glycerol (George & Berger 1966). It is also known that the avian flight muscle contains numerous mitochondria and high concentrations of oxidative enzymes (George & Berger 1966).

The pectoralis muscle of the Rosy Pastor contains two types of fibre, a red, narrow fibre containing numerous mitochondria and high concentrations of fat, lipase and oxidative enzymes and the other a light, broader fibre considerably fewer in number and containing fewer mitochondria and much less lipase and oxidative enzymes (George & Berger 1966). Using histochemical techniques, George & Talesara (1962) showed that the pectoralis muscle fibres of the Rosy Pastor contain considerably higher levels of oxidative enzymes than those of the domestic goose and the domestic fowl. In another study they (1961) observed that the activity of one of the key enzymes in the Krebs cycle, succinic dehydrogenase (SDH), in the Rosy Pastor was higher than that of the several other birds and a bat studied. They also found that towards migration the

SDH activity in the muscle of the Rosy Pastor reached a peak level, twice that of the level recorded during the postmigratory period. On the other hand lipase activity in the muscle was found to be lower in the premigratory phase (Vallyathan 1963). In a study of the particulate fractions and whole homogenate of the pectoralis muscle in the premigratory and postmigratory periods, George & Vallyathan (1964a) observed that lipase activity was lower in the premigratory phase and SDH activity higher than in the postmigratory phase. The experiments were conducted in the early hours of the morning as well as in the evening so as to know if there were diurnal differences. From the results obtained they suggested that fat was synthesized during the night. George & Chandra-Bose (1967) studied diurnal changes in the levels of glycogen and fat in the pectoralis muscle of the Rosy Pastor during the premigratory and postmigratory periods. Glycogen content of the muscle was found to be higher in the evening than in the morning whereas fat content was higher in the morning. The decrease of glycogen during the night and of fat during the day was explained as due to the preferential utilization of the two metabolites, namely glycogen during night and fat during day time. Prior to migration, however they observed that the level of fat in the morning and in the evening was more or less the same. This observation prompted them to suggest that during the premigratory phase when the body fat reserve was being built up, the bird was utilizing carbohydrate for muscular energy by oxidizing pyruvate instead of fatty acid and thereby sparing fat. Phosphorylase activity in the pectoralis muscle of the Rosy Pastor was found to be higher in the premigratory period (Vallyathan & George 1963, 1964). This also supports the above suggestion.

Experiments were conducted to assess the capacity of the muscle for fatty acid oxidation. George & Vallyathan (1964b) showed that the breast muscle homogenate of the Rosy Pastor in the postmigratory phase had a greater capacity for fatty acid oxidation than that in the premigratory phase and that there was greater oxidation of malate in the manometric system in the latter case. In a comparative study of the capacity for fatty acid oxidation by the breast muscle homogenate of the Rosy Pastor in its premigratory phase, and that of a non-migratory starling, *Acridotheres tristis*, George & Iype (1964) found that it was lower in the Rosy Pastor at that time. They suggested that there exists a control system in the Rosy Pastor which minimizes fat utilization during the premigratory period so as to enhance fat storage. Such a control system should obviously be a hormonal system. Experiments are presently being carried out by George and his associates at Guelph with a view to obtaining a clearer understanding of the regulatory mechanisms involving the secretions of the hypothalamus and the endocrine glands which control the various metabolic processes in the body.

The heart muscle is also known to utilize fat as the major fuel for its energy. George & Iype (1961), correlating lipase activity of the cardiac muscle with the rate of heart-beat, showed that the lipase activity in the heart muscle of the Rosy Pastor was lower than that of the non-migratory starling; *Acridotheres tristis*, indicating a slower heart rate in the former as is known to be the case in human marathon runners.

Sustained flight during migration is possible only if there is a copious and continuous supply of the fuel as well as oxygen. Since the transport of oxygen is the function of the red blood cells, seasonal changes in the blood should be expected. Pilo & George (1970b) studied erythropoiesis in the bone marrow and seasonal changes in the haemoglobin content as well as red cell count in the blood of the Rosy Pastor. Increased erythropoiesis was noticed in the bone marrow in the premigratory period. Consequently, a corresponding increase in haemoglobin content as well as red cell count was seen in the blood. A considerable degree of red cell destruction was found in the liver during the postmigratory period.

Studies on the physiological adaptations in the Rosy Pastor have provided interesting and significant leads towards a clearer understanding of the mechanisms of internal regulation and energy metabolism and have also stimulated further research. Research on these lines would undoubtedly lead to the solution of the riddle of bird migration. The wealth of new information expected to emanate in the years ahead would also have far-reaching implications not only in biology but in medical science as well. While we realize these goals, it is necessary and legitimate to recognize the valuable contributions of field ornithologists that formed the foundation for such studies. In bringing forth the present volume, we pay our tribute to a great ornithologist for his monumental contributions to ornithology in general and to ornithology of the Indian subcontinent in particular.

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